

## IMPACT OF CANNIBALISM ON PREDATOR–PREY DYNAMICS: SIZE-STRUCTURED INTERACTIONS AND APPARENT MUTUALISM

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**Abstract.** Direct and indirect interactions between two prey species can strongly alter the dynamics of predator–prey systems. Most predators are cannibalistic, and as a consequence, even systems with only one predator and one prey include two prey types: conspecifics and heterospecifics. The effects of the complex direct and indirect interactions that emerge in such cannibalistic systems are still poorly understood. This study examined how the indirect interaction between conspecific and heterospecific prey affects cannibalism and predation rates and how the direct interactions between both species indirectly alter the effect of the cannibalistic predator. I tested for these effects using larvae of the stream salamanders *Eurycea cirrigera* (prey) and *Pseudotriton ruber* (cannibalistic predator) by manipulating the relative densities of the conspecific and heterospecific prey in the presence and absence of the predator in experimental streams. The rates of cannibalism and heterospecific predation were proportional to the respective densities and negatively correlated, indicating a positive indirect interaction between conspecific and heterospecific prey, similar to “apparent mutualism.” Direct interactions between prey species did not alter the effect of the predator. Although both types of prey showed a similar 30% reduction in night activity and switch in microhabitat use in response to the presence of the predator, cannibalism rates were three times higher than heterospecific predation rates irrespective of the relative densities of the two types of prey. Cumulative predation risks differed even more due to the 48% lower growth rate of conspecific prey. Detailed laboratory experiments suggest that the 3:1 difference in cannibalism and predation rate was due to the higher efficiency of heterospecific prey in escaping immediate attacks. However, no difference was observed when the predator was a closely related salamander species, *Gyrinophilus porphyriticus*, indicating that this difference is species specific. This demonstrates that cannibalism can result in the coupling of predator and prey mortality rates that strongly determines the dynamics of predator–prey systems.

**Key words:** *apparent competition; density-mediated indirect interactions; Eurycea cirrigera; foraging behavior; predator-dependent functional response; Gyrinophilus porphyriticus; ontogenetic niche shift; population dynamics; Pseudotriton ruber; size/stage-structured interaction; trait-mediated interactions; two-prey system.*

### INTRODUCTION

The dynamics of predator–prey systems are determined by the interaction of inter- and intraspecific processes. These interactions, however, are often complex because the populations of predators are generally size structured (Ebenman and Persson 1988, Polis 1991, Persson 1999). Thus, individuals engage in *size-structured interactions* in which the type and strength of the ecological interaction may depend more on the relative size difference between interacting individuals than on their taxonomy. Secondly, because of the size structure within populations, predators are often cannibalistic (Fox 1975a, Polis 1981, Woodward and Hildrew 2002, Woodward et al. 2005), creating complex direct and indirect interactions within and between species that are not possible in populations without cannibalism (Wahlstrom et al. 2000, Persson et al. 2003, Crumrine 2005,

Rudolf 2006, 2007a, b). While there has been considerable progress in predicting the population dynamics of size-structured cannibalistic populations (Ebenman and Persson 1988, Persson et al. 2000, 2003, Claessen et al. 2004), predicting the consequences of cannibalism for the dynamics of communities remains a central challenge (Claessen et al. 2004).

Besides the density-dependent processes in the prey, the dynamics of a predator–prey system strongly depend on three factors: (1) the functional response of predators to prey, (2) density-dependent processes in the predator population, and (3) the direct and indirect effects of alternative prey (Berryman 1992, Abrams and Matsuda 1996). Cannibalistic predator–prey interactions always include two prey types, conspecific and heterospecific prey that are both subject to predation by the same predator. However, the dynamics of such systems cannot be readily inferred from noncannibalistic systems, because one prey type is the predator itself and all three factors can be connected. Previous studies have shown that the functional response for cannibalism is

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negatively related to the density of heterospecific prey: i.e., cannibalism decreases with increasing heterospecific prey density (Fox 1975b, Van Buskirk 1987, Leonardsson 1991, Wagner and Wise 1996, Kerby and Kats 1998, Michaud 2003, Laycock et al. 2006). This also implies that in cannibalistic systems the density-dependent mortality of the predator is directly linked to its consumption of the heterospecific prey, unlike in systems without cannibalism. The density of conspecific prey is also likely to have an indirect positive effect on the heterospecific prey by reducing its mortality via predation. In this case, cannibalism and predation rates would both be indirectly coupled and each would depend on the densities of both prey species. Most previous studies (see Fox 1975b and following, above) have focused solely on the effect of alternative prey on cannibalism rates and they have neglected this possible coupling of cannibalism and predation rates. However, recent theoretical work suggests that it is exactly this coupling that has important consequences for the dynamics of communities (Rudolf in 2007b).

Due to the size structure in cannibalistic predator-prey systems, direct nonpredatory interactions (i.e., competition or behavioral interference) between the conspecific (i.e., small-predator stage) and heterospecific prey are also likely (Hamrin and Persson 1986, Persson 1988, Persson and Greenberg 1990, Taylor et al. 2001, Yasuda et al. 2004, Cameron et al. 2007). Such interactions between prey species could affect the cannibalism and predation rates and create nonlinear interaction effects between conspecific and heterospecific prey densities and the predator (Gurevitch et al. 2000). For example competition could reduce growth rates and thus prolong the time a prey is vulnerable to predation (Wilbur 1988), or the heterospecific prey might respond differently to conspecific prey (i.e., small predators) than to large predators, which can alter its predation risk (Rudolf 2006). Previous studies (e.g., Fox 1975b, Leonardsson 1991, Wagner and Wise 1996, Kerby and Kats 1998, Michaud 2003, Laycock et al. 2006) were generally very short experiments of a few hours duration that altered the density of only one prey type in the presence of the predator and were thus unable to detect such nonlinear interactions resulting from prey-prey and predator-prey interactions.

The goal of this study was to elucidate how direct and indirect interactions between conspecific and heterospecific prey affect the functional relationships of a cannibalistic predator and its prey and the mechanisms that underlie these effects. In particular, I experimentally separated the effects of direct and indirect interactions between a cannibalistic predator, its conspecific prey, and its heterospecific prey to answer three main questions: (1) How are cannibalism and predation rates affected by the relative densities of conspecific and heterospecific prey? (2) Are the predation rates of conspecific and heterospecific prey negatively correlated, indicating a positive indirect interaction between con-

specific and heterospecific prey? (3) Does the direct interaction between prey species alter the effect of the cannibalistic predator? Furthermore, I used additional laboratory experiments to determine the mechanisms that underlie the observed difference in predation risk of conspecific and heterospecific prey and to determine whether this difference was species specific.

## MATERIALS AND METHODS

### *Study species*

Stream salamanders are generalized top predators in fishless headwater streams where they commonly prey on invertebrates and smaller salamander larvae, including conspecifics (Rudolf 2006). *Pseudotriton ruber* is an abundant salamander in the southern Appalachian Mountains (USA). Due to its larval period of three years and a short breeding season, populations are characterized by the coexistence of three distinct size classes that can differ four-fold in size (snout-vent length, 11.74–46.84 mm; mass, 0.035–2.417 g) (*unpublished data*). Previous studies have shown that larvae during their first year are commonly cannibalized by two and three year old conspecifics (Gustafson 1993; *unpublished data*). *Eurycea cirrigera* is the most abundant species of stream salamander in the southern Appalachians, and a common prey for larger salamanders such as *P. ruber* and *Gyrinophilus porphyriticus* (Resetarits 1991, Gustafson 1993, Rudolf 2006). During their larval period of one year (Bruce 1982, 1985), *E. cirrigera* are similar in size to young-of-the-year *P. ruber* larvae and share the same habitats.

### *Direct and indirect interactions of conspecific and heterospecific prey*

This field experiment was designed to estimate the long term functional response of a cannibalistic predator and to test how conspecific and heterospecific prey directly and indirectly affect each others' survival, growth, and behavior under natural conditions. All experiments were carried out at Mountain Lake Biological Station (MLBS), Virginia, USA. Larvae of all species were collected from two headwater streams near MLBS. Details of the location and construction of experimental streams are given by Rudolf (2006) and Resetarits (1991). In brief, experimental streams ( $3.35 \times 0.69 \times 0.36$  m [length,  $L \times$  width,  $W \times$  depth,  $D$ ]) were designed to adequately represent the spatial and temporal heterogeneity found in natural habitats of stream salamanders. These streams were placed on top of a stream bed under a natural canopy of vegetation and received water independently from a collecting tank fed by a natural spring. The water flow of each stream was adjusted initially to 3 L/min but varied depending on rainfall. Streams were tilted at a  $2^\circ$  angle to create a natural water-depth gradient from  $\sim 0$  cm (upstream end) to 20 cm (downstream end). Each stream received a mixture of 60 L of sand and river gravel and 12 flat rocks that were spaced evenly in a zig-zag pattern along

the stream to serve as cover objects, and one large splash rock was placed below the inflow. The top of the units were open to allow colonization by aquatic invertebrates and to permit arthropods and leaf litter to fall into the streams. An overhanging 10-cm lip on the inside edge of the streams prevented salamanders from escaping. Water flow was initiated two weeks before the start of the experiment to allow colonization of the streams by a variety of invertebrates that serve as alternative prey for salamander larvae (Rudolf 2006).

The experiment was a  $2 \times 2$  factorial, randomized, complete block design in which similar sized larvae of *E. cirrigera* (snout-vent length, SVL =  $14.05 \pm 0.87$  mm [mean  $\pm$  SD]; range, 11.1–15.62 mm) and small *P. ruber* (SVL =  $13.92 \pm 0.87$  mm; range, 11.22–15.61 mm) were exposed to two ratios (10:20 and 20:10 individuals) of conspecifics:heterospecifics in the presence (5 individuals) or absence of large cannibalistic *P. ruber* (SVL =  $38.8 \pm 2.11$ ; range, 35.9–44.7 mm). This substitutive design manipulated the relative abundance of conspecific and heterospecific prey while keeping the total salamander prey density constant to avoid confounding effects due to changes in total prey density. Densities for each species and size class represent low to mean natural densities found in headwater streams at MLBS (Rudolf 2006; unpublished data). Larvae of *E. cirrigera* and small *P. ruber* were each separated into 10 size classes. Depending on the respective ratio treatment, either one (10 larvae, giving a density of 4.3 individuals/m<sup>2</sup>) or two individuals (20 larvae, giving a density of 8.7 individuals/m<sup>2</sup>) of each size class and species were assigned randomly to each stream. This assured that both the size range and size average were identical across treatments and densities. Similarly, large *P. ruber* were divided into five size classes and one individual of each size class was randomly assigned to a stream with the respective predator treatment. Size classes used in the experiment represent the range found in natural populations. Experiments started on 2 June 2005 and ended after six weeks on 12 July 2005 when the first small *E. cirrigera* entered metamorphosis. At the end of the experiment, streams were sampled for survivors for three consecutive days to make sure that all individuals in the streams were recovered.

**Growth and survival.**—The SVL and mass of all individuals were measured prior to the experiment and after termination of the experiment when individuals had emptied their guts in the laboratory. Large *P. ruber* were photographed at the beginning and at the end of the experiment. At this stage, larvae have a unique pattern of pores on the back of their heads that can be used to identify individuals. Growth rates of large *P. ruber* were calculated for each individual as  $(\ln[\text{final mass}] - \ln[\text{initial mass}])/t'$ , with  $t'$  = duration of the experiment (=40 d). Small *P. ruber* and *E. cirrigera* could not be identified individually. Thus, growth rates were calculated using the difference between initial and final stream means. All growth analyses were based on

stream means. Mortality rates,  $m$ , of both prey types were calculated assuming the survival model:  $N_t = N_0 e^{-mt}$  and solving for  $m = -\ln(N_t/N_0)/t$ , with  $N_t$  and  $N_0$  = final number of survivors and initial density respectively. All large *P. ruber* survived.

**Activity and microhabitat surveys.**—To determine treatment effects on the individual behavior of a species and stage, I monitored night and day activity every seven days and habitat use every other week for all species and stages. Streams were searched visually with a flashlight by slowly moving from the downstream to the upstream end. Individuals were defined to be active if they were visible above the substrate on first sighting. Day and night censuses were carried out at 10:00 and 22:00 hours, respectively, and their order was alternated between censuses. The search order of blocks and units within blocks was randomly assigned prior to each census. The proportional activity was calculated for each census period ( $t$ ) as  $(\text{number of larvae observed at } t)/(\text{number of larvae present at } t)$ . The number of larvae alive at time  $t$  ( $N_t$ ) was estimated from the predation model  $N_t = N_0 e^{-mt}$ , with  $t$  = days since start of the experiment and the stream specific mortality rate,  $m$  (see *Growth and survival*, above). For the microhabitat use, each stream was divided into 14 equal sections, and the relative abundance within each section (number of larvae in section  $x$ /total number of larvae observed) was recorded for each species and stage. Microhabitat surveys were performed similar to the activity census with the difference that cover rocks were lifted carefully to check for hidden larvae. Rocks could generally be lifted and returned without triggering larval movement. For each stream, the mean of all three microhabitat observations was used in the analyses and arcsine transformed to meet normality assumptions.

**Statistical analysis.**—Two weeks after the start of the experiment, I noticed the first large *P. ruber* with clear signs indicating the initiation of metamorphosis. The laboratory experiments (see below) indicated that large *P. ruber* that displayed phenotypic signs of metamorphosis did not consume small salamander larvae. Thus, beginning from this period I monitored streams every five days and recorded the state of each large *P. ruber* (i.e., metamorph or non-metamorph). This allowed me to estimate the effective predation risk, by calculating the number of “predator-days” for each stream (= total number days a predator showed no signs of metamorphosis summed for all five predators within a stream). The total number of consumed prey significantly increased with predator-days (regression analysis:  $F_{1,6} = 8.48$ ,  $P < 0.027$ ,  $R^2 = 0.586$ ) and was thus included in the analyses of mortality and growth rates as a covariate instead using the simple presence or absence of large *P. ruber*. Mortality, mass and SVL growth rates were analyzed using a general linear mixed model (the Proc Mixed procedure [SAS Institute 2003]) with prey ratio as a fixed factor, predator-days as covariate, and block as a random effect. If the interaction term of the

predator-days and ratio treatments was not significant, the interaction term was removed from the model and a final analysis was carried out with adjusted degrees of freedom (Quinn and Keough 2004). There was no relation between predator days and any behavioral measurement. Thus, day activity, night activity and microhabitat use were analyzed with a repeated-measures general-linear mixed model (Proc Mixed procedure), with prey ratio and presence or absence of large *P. ruber* as fixed effects, block as a random effect, and time of observation as a repeated factor for the activity analysis and stream section as a repeated factor in the microhabitat analysis to account for the covariance of repeated observations or sections within a stream. The covariance structure for each repeated-measure analysis was determined using the model with the lowest AIC values (Littell et al. 1998). Block effects were tested using a one-tailed log-likelihood ratio test (Littell et al. 1996). In situations where block effects were not significant ( $P > 0.12$ , see Appendix A) block degrees of freedom were pooled with the error-term degrees of freedom for the final analysis. This did not alter the general results of the analyses. To account for the variation in the predation risk in the correlation analysis of predation rates for conspecific and heterospecific prey, a regression was performed with predator days as independent variables and number of consumed prey of conspecific or heterospecific as dependent variable. The residuals of the regression for each prey type were then used to test for a correlation of the predation rates of both prey types.

#### *Metamorph predation experiment*

I also conducted a separate experiment to quantify whether metamorphosis affected the predation rate of *P. ruber*. To do this I compared the predation rate of large *P. ruber* individuals that did and did not show clear signs indicating the initiation of metamorphosis. One large *P. ruber* was added to a  $12 \times 11 \times 8$  cm ( $L \times W \times D$ ) opaque plastic box with 1100 mL of stream water and allowed to prey on one conspecific and one heterospecific prey that were matched by size for 10 days. Nine replicates were performed with each metamorphic status of *P. ruber*. Each box contained one small rock in one corner and one 5-cm PVC half-pipe in the opposite diagonal corner to serve as cover objects. Each box was tilted to create a water depth gradient of 1 cm to 5 cm to allow metamorphs to leave the water. Boxes were checked daily and consumed individuals were replaced immediately. Differences between treatments were analyzed using a Mann-Whitney *U* test.

#### *Laboratory choice experiments*

I conducted a series of laboratory experiments to identify the specific factors that may contribute to any differences in cannibalism and predation rates observed in the field experiments. In the first experiment, I tested whether differences in predation risk of conspecific and

heterospecific prey would persist in the absence of habitat structure. One large *P. ruber* was placed in an opaque plastic box ( $40 \times 22 \times 25$  cm [ $L \times W \times D$ ] and 8 cm water depth) together with one small conspecific and one heterospecific prey individual of similar size. Size classes were identical to those used in the field experiment. Large *P. ruber* were kept in a transparent plastic cup for five minutes after addition of the prey to allow larvae to acclimatize before the beginning of the experiment. Experiments were checked for survivors first after 3 h and then every 12 h and terminated as soon as one larva was consumed, or after five days, whichever occurred first. The experiment was repeated 50 times. This replication was chosen based on a priori power analysis (using a binomial distribution) and allowed a detection of a small effect size (difference from equal preference) of 0.15 or 0.2 at a significance level of  $\alpha = 0.05$  with a power of 0.73 and 0.92, respectively.

To test if the predation risk was species specific, I conducted a second experiment that was identical to the first except that I used *Gyrinophilus porphyriticus*, another large salamander, as the cannibalistic predator and *E. cirrigera* again as the prey. Experiments were carried out during June–September in 2005 and 2006 whenever the larvae of the required size class could be obtained from the natural streams. A two-tailed binomial test was used to test if the predation risks for conspecific and heterospecific prey were unequal.

The first laboratory experiment could not distinguish if the difference in the mortality risk of both prey types was due to differences in the behavior between prey species or an innate preference of the predator for a specific prey species. Thus, I performed a third choice experiment to test if large *P. ruber* display a preference for conspecifics. In this experiment, one large *P. ruber* was placed in a box ( $40 \times 22 \times 25$  cm and 8 cm water depth) that was divided in two equal 20-cm sections that each contained one transparent, water filled, and perforated polyethylene plastic Ziploc® bag attached to the end of a section. One small *P. ruber* and one *E. cirrigera* larva of similar size were each randomly assigned to a different bag within a box. The prey individuals were thus confined to opposite sides, while being clearly visible and chemically detectable. During the experiment, multiple large *P. ruber* attacked a prey individual in a bag, indicating that they clearly recognized the potential prey. Large *P. ruber* were added one day prior to the addition of the prey for acclimatization. After the prey was introduced, I recorded the position of the head of large *P. ruber* in one out of the two sections every 30 minutes for five consecutive hours, resulting in a total of five day and five night observations. The experiment was replicated 27 times based on the number of available large *P. ruber* on 22 July 2006. Differences between the numbers of observation spent in the section with conspecific or heterospecific prey were analyzed using a one-sample *t* test.

All laboratory experiments were carried out in a climate controlled room at MLBS at 13°C and a 12:12

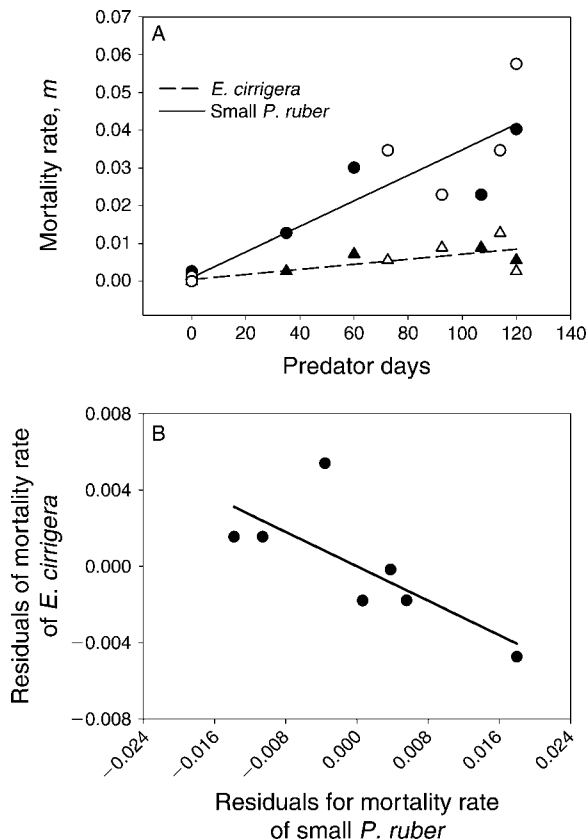


FIG. 1. Mortality data. (A) Mortality rates of conspecific prey (small *Pseudotriton ruber*) and heterospecific prey (*Eurycea cirrigera*) in relation to the number of predator days. Predator days indicate the realized predation risk by large *P. ruber* after accounting for nonpredatory metamorphs. The solid and the dashed lines indicate the regression of the mortality rates vs. predator days pooled across density treatments for small *P. ruber* (circle) and *E. cirrigera* (triangle), respectively. Solid symbol = 10 small *P. ruber* + 20 *E. cirrigera*; open symbol = 20 small *P. ruber* + 10 *E. cirrigera*. (B) Correlation between the mortality rate of conspecific and heterospecific prey within a stream with predators present. The residuals were used to account for the variation in predation risk and were obtained from a regression analysis for each prey type with the mortality rate ( $m$ ) as the dependent variable and predator days as the independent variable. The significant correlation (Spearman's rho,  $r = -0.9$ ,  $P = 0.006$ ,  $N = 7$  replicate streams) indicates that cannibalism and predation rates are negatively correlated. One significant outlier was not included in the analysis (see *Results* for further details).

day : night cycle, and with fresh water collected from a nearby first-order headwater stream. All boxes were set up in a complete randomized design in a single shelf rack and visually separated by cardboard partitions.

## RESULTS

### Metamorph predation rates

The experiment showed that none of the metamorphs consumed prey, which was significantly (Mann-Whitney  $U$  test:  $Z = -3.053$ ,  $P < 0.0001$ ,  $N = 18$  salamanders)

lower than the number of prey consumed by non-metamorphs ( $1.9 \pm 1.3$  [mean  $\pm$  SD]).

### Stream experiments

Mortality rates of small *Pseudotriton ruber* ( $F_{1,13} = 78.94$ ,  $P < 0.0001$ ) and *E. cirrigera* ( $F_{1,13} = 28.34$ ,  $P = 0.0001$ ) strongly increased with predator days (Fig. 1A). Mortalities of both prey types were not affected by the ratio of conspecific vs. heterospecific density (small *P. ruber*,  $F_{1,13} = 0.3$ ,  $P = 0.60$ ; *E. cirrigera*,  $F_{1,13} = 0.01$ ,  $P > 0.90$ ) or the interaction of ratio and predator-days (small *P. ruber*,  $F_{1,12} = 1.18$ ,  $P = 0.297$ ; *E. cirrigera*,  $F_{1,12} = 0.09$ ,  $P > 0.75$ ) (Fig. 1). These constant predation coefficients across ratios indicate that predators showed no switching behavior (i.e., changing of prey preference). Note that the number of consumed conspecific and heterospecific prey was still affected by the ratio treatment and was significantly lower when the respective prey type was less frequent (conspecific prey,  $F_{1,12} = 65.04$ ,  $P < 0.0001$ ; heterospecific prey,  $F_{1,12} = 5.07$ ,  $P < 0.05$ ). I used Manly et al.'s (1972) preference index ( $\alpha$ ) corrected for prey depletion to test for a potential preference (no preference is indicated by  $\alpha = 0.5$ , with a possible range of  $0 \leq \alpha \leq 1$ ) of the predator for either prey species. *P. ruber* showed a strong preference for conspecific prey ( $\alpha = 0.81 \pm 0.086$  [mean  $\pm$  SD], range 0.72–0.96) compared to heterospecific prey ( $t_7 = 10.31$ ,  $P < 0.0001$ ), indicating that cannibalism was four times higher than heterospecific predation. This preference resulted in a significant convergence of the densities of both prey types in treatments with a high density of small *P. ruber* ( $t_3 = 4.74$ ,  $P < 0.02$ ) and a significant divergence in treatments with a low density of small *P. ruber* ( $t_3 = 3.69$ ,  $P < 0.035$ ) (Fig. 2).

Despite the overall preference for conspecifics, the number of consumed conspecific and heterospecific prey within a stream were negatively correlated (Pearson's  $r_7 = -0.90$ ,  $P = 0.005$ ). A similar analysis for the mortality rates ( $m$ ) showed also a significant negative correlation (Spearman's  $r_7 = -0.75$ ,  $P = 0.05$ ) (Fig. 1B), indicating a positive indirect interaction between conspecific prey and heterospecific prey. In that analysis, one replicate was a significant outlier ( $t_6 = 1.96$ , one-tailed  $P < 0.05$ ) where the number of total prey consumed was less than half than the next lowest replicate and it was thus removed from the analysis. This was also the replicate with the highest number of metamorphs (i.e., lowest number predator-days).

The presence of large *P. ruber* reduced the growth rate of small *P. ruber* on average by 59.2% for mass ( $F_{1,13} = 7.15$ ,  $P = 0.0191$ ) and 44.1% for snout-vent length (SVL) ( $F_{1,13} = 10.13$ ,  $P = 0.0072$ ) (Fig. 3). The growth rate of *E. cirrigera* was also reduced in the presence of large *P. ruber* on average by 23.2% ( $F_{1,13} = 8.21$ ,  $P = 0.0133$ ) for mass and 23.2% for SVL ( $F_{1,13} = 13.09$ ,  $P = 0.0031$ ) (Fig. 3). For both species, the size-distribution did not change (ANOVA for skewness:  $P > 0.36$ ). The ratio of conspecific vs. heterospecific density and the interaction

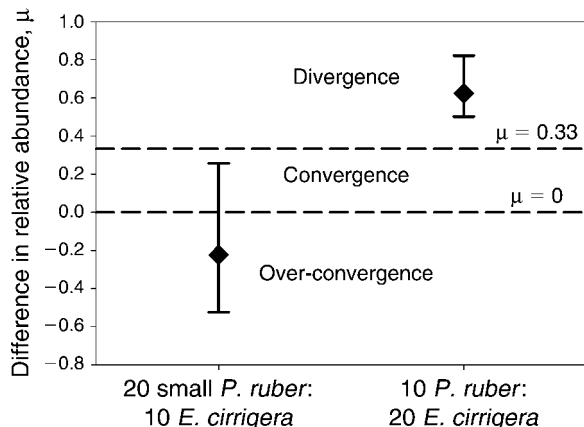


FIG. 2. Mean (and 95% CI) difference in relative abundance between conspecific (*Pseudotriton ruber*) and heterospecific (*Eurycea cirrigera*) prey species at the end of the experiment for each ratio treatment;  $\mu = [(N_{E. cirrigera} - N_{P. ruber}) / (N_{E. cirrigera} + N_{P. ruber})]$ , with  $N_i$  = number of survivors of prey species  $i$ . Values of  $\mu > 0.33$  (= initial relative difference in abundance) indicates divergence of the abundances of both prey types,  $0 < \mu < 0.33$  convergence, and  $\mu < 0$  over-convergence. There was a significant convergence in treatments with high frequency of small *P. ruber* ( $t$  test:  $t = 4.74, P = 0.0178, df = 3$ ), and significant divergence in treatments with low frequency of *P. ruber* ( $t$  test:  $t = 3.69, P = 0.0345, df = 3$ ).

of the ratio and predator treatment had no effect on growth rates of small *P. ruber* or *E. cirrigera* (for all ratios:  $F_{1,13} < 0.24, P > 0.60$ , for all ratio  $\times$  (predator days):  $F_{1,12} < 1.08, P > 0.30$ ) (Fig. 3). Overall, the growth rate of small *P. ruber* was 38.2% lower for mass (paired  $t$  test:  $t = 2.87, df = 15, P < 0.05$ ) and 48.7% for SVL (paired  $t$  test:  $t = 5.72, df = 15, P < 0.0001$ ) than the growth rates of *E. cirrigera*. This difference was similar in the presence and absence of large *P. ruber* ( $t$  test; mass,  $t_{14} = 0.62, P > 0.50$ ; SVL,  $t_{14} = -0.84, P > 0.40$ ). Growth rates of large *P. ruber* were not affected by the prey ratio treatment (mass,  $F_{1,6} = 0.97, P > 0.35$ ; SVL,  $F_{1,6} = 0.44, P > 0.50$ ). In amphibians, individuals stop feeding and decrease in size and mass during metamorphosis. An analysis with only non-metamorphs showed that growth rates increased with predator-days, but this was only significant for snout-vent length (SVL,  $F_{1,6} = 20.93, P < 0.004$ ; mass,  $F_{1,6} = 3.96, P > 0.09$ ).

The night activity of small *P. ruber* was on average significantly reduced by 37.0% in the presence of large *P. ruber*, but increased between the first two census periods in the absence of the predator, resulting in a significant interaction term of time and predator treatment (Appendix B). Day activity of small *P. ruber* was significantly affected by the interaction of time and the presence of large *P. ruber* largely due to lower activity in the presence of large *P. ruber* during the first census period (Fig. 4; Appendix B). *E. cirrigera* also significantly reduced their night activity on average by 29.5% in the presence of large *P. ruber*, but unlike small *P. ruber* increased day activity by 23.3% in the presence of

predators (Fig. 4; Appendix B). Night activity of *E. cirrigera* increased in the absence of predators, resulting in a significant interaction of predator treatment and time (Appendix B). The activities of both prey species was not affected by the prey ratio (Appendix B). Overall, *E. cirrigera* always had a higher day activity (without predators, 1.9 times higher, paired  $t$  test,  $t_7 = 5.12, P < 0.001$ ; with predators, 2.9 times higher,  $t_7 = 9.47, P < 0.0001$ ) and night activity (without predators, 1.3 times higher,  $t_7 = 4.49, P < 0.003$ ; with predators, 1.5 times higher,  $t_7 = 2.66, P < 0.03$ ) than small *P. ruber* (Fig. 4). The difference ([mean activity of small *P. ruber*] - [mean activity of *E. cirrigera*]) remained the same for the night activity ( $t_{14} = 0.10, P > 0.90$ ), but increased significantly by 83.2% for the day activity in the presence of predators ( $t_{14} = -3.03, P < 0.01$ ). The activity of large *P. ruber* did not differ significantly between both prey density ratios (Mann-Whitney  $U$  test: day,  $Z = -0.16, P > 0.85$ ; night,  $Z = -0.15, P > 0.85, N = 8$ ).

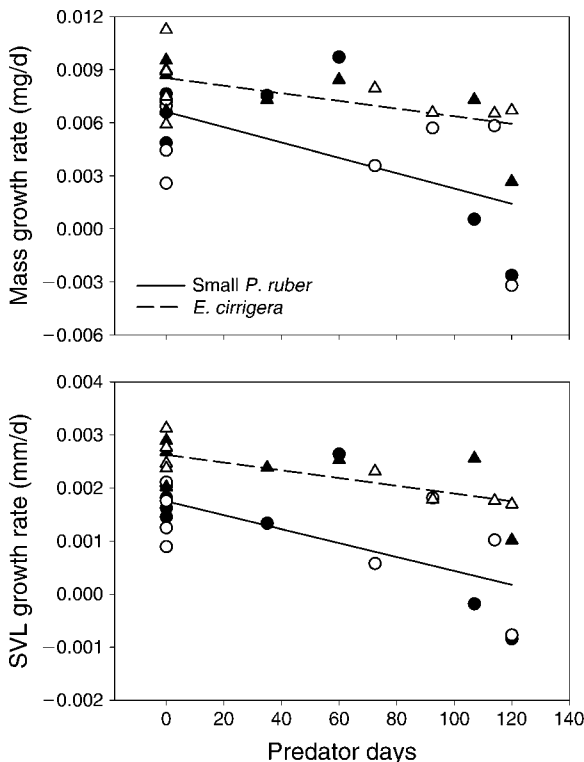


FIG. 3. Growth rates for mass and snout-vent length (SVL) of conspecific prey (small *Pseudotriton ruber*; circles) and heterospecific prey (*Eurycea cirrigera*; triangles) in relation to the predation risk by large *P. ruber*. Predator days indicate the predation risk within a stream after correcting for nonpredatory metamorphs of large *P. ruber* (see *Materials and methods* for details) (0 = no predator treatment). Growth rates are based on stream means. The solid and the dashed lines indicate the regression of the growth rates vs. predator days pooled across density treatments for small *P. ruber* and *E. cirrigera* respectively. Solid symbols = 10 small *P. ruber* + 20 *E. cirrigera*; open symbols = 20 small *P. ruber* + 10 *E. cirrigera*.

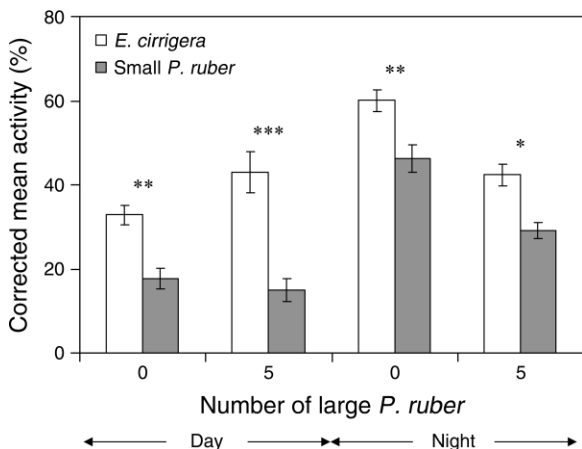


FIG. 4. Day and night activity of both conspecific (small *Pseudotriton ruber*) and heterospecific (*Eurycea cirrigera*) prey in treatments with and without predators (large *P. ruber*). Activity was measured as the number of actively foraging individuals per stream visible above the substrate. Activity from six repeated observations during the experiment was analyzed using a repeated-measures mixed model. Proportional activity was corrected for the dead individuals for each observation period using the estimated mortality rate,  $m$ , and a time discrete predation model ( $N_t = N_0 e^{-mt}$ ). Significant differences in the specific differences between pairs of *E. cirrigera* and *P. ruber* are indicated: \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.0001$  (paired  $t$  test); data are means  $\pm$  SD.

The significant interaction of predator presence and stream section for the microhabitat use of small *P. ruber* and *E. cirrigera* (Appendix C) indicates that both prey species altered their microhabitat use in response to the presence of large *P. ruber*. The microhabitat use of both prey species also differed between ratios (significant interaction of ratio  $\times$  stream section), but there was no interaction of ratio and predator treatment (Appendix C). In the absence of large predators, both prey types preferred the very downstream end, but this section was also strongly preferred by large *P. ruber* (Fig. 5). Thus, *E. cirrigera* moved to the middle and upstream sections of the stream and small *P. ruber* to the upstream sections of the stream in the presence of large *P. ruber* (Fig. 5). Note that the peak in large *P. ruber* density in the mid-upstream section (Fig. 5) was caused by nonpredatory metamorphs that seemed to prefer this section across streams. To test if both prey types differed in the microhabitat overlap with predators, I used the absolute differences between relative abundance of a prey type and the predator as a measurement of overlap, i.e.,

$$\frac{1}{14} \sum_{i=1}^{14} |[(\text{relative abundance of large } P. \text{ ruber in section } i) - (\text{relative abundance of a prey type in section } i)]| / 14.$$

This was calculated for each of three observations, and the mean of all three calculations were used in the analysis. There were no significant differences (paired  $t$  test,  $t_7 = -0.16$ ,  $P > 0.85$ ) in the microhabitat overlap

with predators between small *P. ruber* ( $11.12\% \pm 0.02\%$  [mean  $\pm$  SD]) and *Eurycea* ( $11.13\% \pm 0.01\%$ ).

Choice experiments

In the first choice experiment small *P. ruber* were consumed in 71% of the total predation events ( $N = 45$ ) and *E. cirrigera* in 29%, resulting in a 2.5 times higher predation risk for conspecifics (two-tailed binomial test:  $Z = -2.83$ ,  $P < 0.005$ ,  $N = 45$ ). This indicates that the difference in mortality observed in the field experiment was not due to differential use of microhabitat. In the same experiment, but with *Gyrinophilus porphyriticus* as the predator, both conspecific *G. porphyriticus* and heterospecific *E. cirrigera* were each consumed in 50% of all predation events ( $N = 38$ ), indicating an equal predation risk (two-tailed binomial test:  $Z = 0.0$ ,  $P = 1.00$ ,  $N = 38$ ).

In the second choice experiment, large *P. ruber* were found on the side with conspecific on average  $49.3\% \pm 36.4\%$  [mean  $\pm$  SD] of all observations and  $50.7\% \pm$

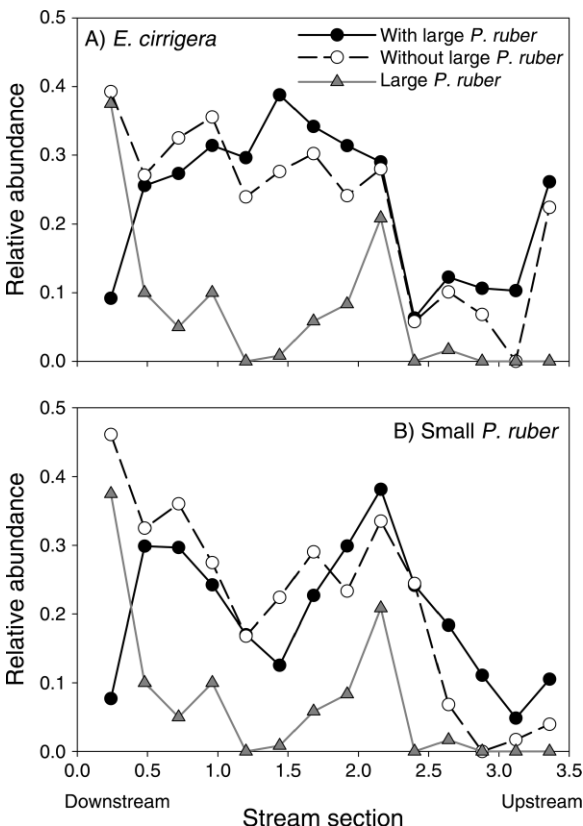


FIG. 5. Average microhabitat use of (A) heterospecific prey (*Eurycea cirrigera*) and (B) conspecific (small *Pseudotriton ruber*) prey in the presence and absence of predators (large *P. ruber*). Relative abundance was measured as the number of individuals within 1 out of 14 sections divided by the total number of individuals observed within a stream. Data are the averages of three observations, and different ratio treatments were pooled for clarity of presentation (there was no interaction effect between ratio and predator treatment).

36.4% observations on the side with heterospecific prey, indicating no innate preference of large *P. ruber* for conspecifics (two-tailed one sample *t* test:  $t = -0.106$ ,  $df = 26$ ,  $P > 0.9$ ).

#### DISCUSSION

##### *Cannibalistic-mediated indirect interactions and the coupling of predation and cannibalism rates*

There is increasing evidence that cannibalism alters the dynamics of predator–prey interactions and even of whole ecosystems (Holyoak and Sachdev 1998, Wahlstrom et al. 2000, Persson et al. 2003, Claessen et al. 2004, Rudolf 2006, 2007a, b). This is often due to the size-structured indirect interactions (density mediated or behavioral mediated) that can result from cannibalism (Sih 1982, Leonardsson 1991, Biro et al. 2003, Bystrom et al. 2003, Rudolf 2006). The negative correlation between per capita cannibalism and predation rates observed in this study demonstrates another indirect interaction: a positive cannibalistic (density)-mediated indirect interaction between conspecific and heterospecific prey. Previous studies have shown that the density of heterospecific prey reduces cannibalism rates (e.g., Fox 1975b, Leonardsson 1991, Wagner and Wise 1996, Kerby and Kats 1998, Michaud 2003, Laycock et al. 2006). To the best of my knowledge, however, this study presents the first experimental evidence of a coupling (i.e., negative correlation) of the per capita predation and cannibalism rates indicating a mutual, positive, indirect interaction between conspecific and heterospecific prey. In three-species systems of one predator and two species of prey, such positive mutual indirect interactions are commonly called “apparent mutualism” (Holt 1977) and have important consequences for community dynamics (Holt and Lawton 1993, Abrams and Matsuda 1996, Bonsall and Hassell 1997, Rudolf and Antonovics 2005). Likewise, recent theoretical work shows that such positive indirect interaction resulting from cannibalism can also have important long-term consequences such as reducing the strength of top-down trophic cascades, altering how enrichment affects the density of the predator and the prey, and stabilizing population dynamics (Rudolf 2007b).

Cannibalism rates were 3 times higher than predation rates. Thus, when assuming a type II functional response one would expect to see a reduction in the per capita mortality rate of each prey type when its relative frequency is low. The results did not show a significant effect of the ratio treatment on the predation rates, but the number of consumed conspecific and heterospecific prey was still significantly different between ratio treatments. The correlation analysis, however, focused on the immediate relationship of the predation rate within a stream and is thus more likely to detect the expected negative correlation. This analysis is also more powerful because it uses the actual number of consumed individuals, which directly determines the time spent handling prey. This suggests that a possible explanation

for this lack of significance might be the high variation due to differences in the predation risk (due to metamorphosis of predators) across the different replicates within a treatment relative to the magnitude of the predation rates. Using higher total prey densities and ensuring that predation risk is more constant in future experiments might overcome the problem of the high variation.

The observed negative coupling of predation and cannibalism rates can easily be explained by predator saturation (i.e., a Holling Type II functional response [Holling 1959]); because a predator cannot consume a conspecific prey while it “handles” (e.g., attacks, consumes, digests) a heterospecific prey and vice versa (Rudolf 2007b). Stream salamanders have relatively long handling times, largely due to long digestion times (*unpublished data*), which could explain why this effect appeared even at relatively low consumption rates. With such a functional response we would always expect a short-term positive indirect interaction between prey species. The long-term effects, however, will depend on the numerical response of the predator (Holt and Lawton 1994, Abrams and Matsuda 1996). Apparent competition between both prey types can occur if the predator density increases proportionally with an increase in either prey type. Cannibalistic systems, however, differ from three species systems because the density-dependent mortality of the predator (and thus its numerical response) is directly related to the respective densities of the predator and the prey. Cannibalism could promote the survival of the large predator class in times of food scarcity, which could result in a small short term apparent competition effect. However, the simultaneous reduction in the recruitment rate due to cannibalism would prevent an increase in the predator population and thus make apparent competition on the long term unlikely. This is the reason why the positive short-term effect observed in this study will also have a positive long-term effect (Rudolf 2007b). Given that most predators show some sort of saturating functional response (Hassel 1978), this positive indirect interaction can be expected for most cannibalistic systems.

##### *Cannibalism vs. predation and predator–prey coexistence*

Both *Eurycea cirrigera* and *Pseudotriton ruber* are omnivores that are likely to compete for food resources. In this case, theory suggests that, in the absence of other mechanisms, coexistence of both species is difficult (Holt and Polis 1997). However, recent theoretical work indicates that cannibalism can strongly promote their coexistence, especially if the mortality rate due to cannibalism is sufficiently larger than the heterospecific predation rate (Rudolf 2007a). In my present study, cannibalism was about 3 times higher than heterospecific predation under natural conditions. Indeed, the difference in the cumulative mortality will be even larger since the conspecific prey had a much lower growth rate than

heterospecific prey. Thus, conspecifics prey are subject to predation more than twice as long before reaching an invulnerable size class. The results also showed that the mortality of both the small predator stage and the prey was proportional to the respective densities. Such density-dependent regulation of the predator and prey mortality should strongly stabilize predator–prey systems.

Another factor that needs to be considered for the long-term dynamics of the system is the respective efficiency of the prey and the predator in converting the resource into biomass (Briggs and Borer 2005). The difference in the growth rates of the small-predator stage and the prey observed in this study indicates that the heterospecific prey is much more efficient in converting the shared resource into body mass. It is likely that this is due to the generally higher activity of the heterospecific prey, if activity is positively related to encounter rates with prey (Werner and Anholt 1993). The differences in the mortality and conversion efficiencies of conspecific and heterospecific prey could explain the high abundance of *E. cirrigera* relative to *P. ruber* in nature (*unpublished data*). Interestingly, this difference in energy conversion is consistent with the hypothesis that due to genetic covariance between developmental stages, predators will often be the inferior competitor to their similar-sized prey (Werner and Gilliam 1984, Persson 1988). If this pattern is generally true, such differences would further promote the coexistence of the cannibalistic predator and the prey and explain why intraguild predation systems are so common in natural communities (Rudolf 2007a).

While there are other examples where cannibalism rates are higher than heterospecific predation rates (Leonardsson 1991, Persson and Eklov 1995, Yasuda et al. 2004, Burgio et al. 2005), the relative difference in predation and cannibalism rates seems to be species specific and can vary considerably even between closely related species. For example, *Gyrinophilus porphyriticus* and *P. ruber* are in the same subfamily, yet the present study shows that *G. porphyriticus* showed no difference in cannibalism and predation rate, while cannibalism was 3 times more likely in *P. ruber* under the same conditions. Similarly, in ladybird beetles and *Anolis* lizards, some species show a higher attack rate for heterospecifics than conspecifics, while others show no difference, or a much higher attack rate for conspecifics (Gerber and Echternacht 2000, Yasuda et al. 2001, Burgio et al. 2005). However, the underlying mechanisms that led to the difference in cannibalism and heterospecific predation rate are often unknown.

My present study gives some insight into potential mechanisms. Both prey species reduced their night-foraging activity and spent more time in refuges at a time when large *P. ruber* are most active. Furthermore, both prey species also altered their habitat use and both were equally efficient in avoiding spatial overlap with the predators. Thus, both conspecific and heterospecific

prey showed similar antipredator behavior, suggesting that the difference in cannibalism and predation rates was not due to different antipredator responses associated with the presence of the predator. The laboratory experiments suggest that cannibalism rates were not higher due to environmental components or innate preference of the predator. This suggests that the heterospecific prey was either more efficient in escaping the immediate attacks of the predator due to physiological differences (e.g., the swimming-burst speed), or showed a different antipredator behavior in direct response to the immediate attack of the predator. However, further experiments are required to determine why they are more efficient and how general these results are across species.

#### *Intra- and interspecific size-structured predator–prey interactions*

In systems with two prey species and one predator, direct interactions between the prey species could alter the effect of the predator and vice versa (Wilbur 1997, Gurevitch et al. 2000). The field experiment showed no interaction effect between prey ratio and predator treatment for any of the response variables of either prey species. This indicates that the direct interaction between prey species did not alter the effect of the predator. The reason for this can readily be inferred from the substitutive design of the experiment. It shows that the ratio of the prey density had no effect on the mortality, growth, or activity rates of either prey species. This suggests that the two prey species are substitutable. If both prey types are substitutable, we would not expect that changes in the relative prey densities alter the effect of the cannibalistic predator. However, in systems where conspecific and heterospecific prey are not substitutable (Olson et al. 1995) or when the substitutability of two species might change with size (Griffen and Byers 2006), interaction effects might arise. Future studies that examine how the emergent effects of direct and indirect size-structured interactions change with relative abundances and size differences will provide important insight into the dynamics of communities.

There is ample evidence that indirect interactions are common, and have important consequences for the dynamics in systems with three or more species (Wootton 1994, Schmitz 1998, Preisser et al. 2005, Vance-Chalcraft and Soluk 2005). The present study adds a new example to the previous theoretical and empirical evidence (e.g., Wahlstrom et al. 2000, Nilsson 2001, Persson et al. 2003, Crumrine 2005, Rudolf 2006, 2007a, b) that size-structured indirect interactions resulting from cannibalism can have a similar profound impact on the dynamics of communities. Given that cannibalism and size-structured interactions are ubiquitous in natural food webs (Fox 1975a, Polis 1981, 1991, Persson 1999, Woodward and Hildrew 2002, Woodward et al. 2005), there is a strong incentive for ecologists to

measure and incorporate such interactions to reliably predict the dynamics of communities.

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#### APPENDIX A

Results of test of random block effects for survival, growth, activity, and microhabitat variables for conspecific prey (*Eurycea cirrigera*), heterospecific prey (small *Pseudotriton ruber*), and predators (large *P. ruber*) (*Ecological Archives* E089-099-A1).

#### APPENDIX B

Repeated-measures analyses on treatment and time effects on relative activity (corrected for mortality) of heterospecific prey (*Eurycea cirrigera*) and conspecific prey (small *Pseudotriton ruber*) (*Ecological Archives* E089-099-A2).

#### APPENDIX C

Repeated-measures analyses on proportional microhabitat use of heterospecific prey (*Eurycea cirrigera*) and conspecific prey (small *Pseudotriton ruber*) (*Ecological Archives* E089-099-A3).